

Molecular population genetics in the species of *Shorea* (Dipterocarpaceae)

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Genetic variation in natural population of forest tree species is strongly influenced by historical and ongoing evolutionary forces, such as mutation, genetic drift, gene flow and natural selection. Since genetic variation is source of adaptation of organisms and its loss is thought to increase the extinction probability, it is important to characterize genetic variation in present natural populations and its changes over a long geological period. Tropical rain forests are characterized by high species diversity of trees, and so each recognized species survives in exceptionally low population density. Coexistence of the closely related species contributes high species diversity at the small spatial scale. The extremely low density of tropical forest trees and their unique mating systems are notable, and very different from those of temperate forest trees. Here, we report the extents and patterns of genetic polymorphisms and genetic divergences in the Southeast Asian *Shorea* species.

Shorea is the largest genus in Dipterocarpaceae and consists of about 200 species. To refine systematics of this economically and ecologically important group, molecular phylogenetic study was conducted based on the analyses of nucleotide sequences of chloroplast and nuclear genes. Results of the phylogenetic analyses were mostly consistent with the Ashton's classification, and four known timber groups (Red Meranti, Selangan Batu, White Meranti, and Yellow Meranti) were shown to be well-separated genetically. However, closely related species within Red Meranti shared genetic variation, and the sequence divergence among species were generally low. This suggests recent diversification of the *Shorea* species.

Our phylogenetic studies of the closely related species of *Shorea* highlighted their complicated evolutionary history. The shared genetic variation could be attributed to persistence of variation that was present in the ancestral species (ancestral polymorphism). However, the low level of divergence and general flowering also suggest that closely related species could have exchanged genes through hybridization (gene introgression). Therefore, it is necessary to discern the two possible causes, ancestral polymorphisms and gene introgression, of the shared variation among the species. For this purpose, we examined nucleotide sequences of four nuclear genes (*PgiC*, *GBSSI*, *Met*, and *Gdh*) and chloroplast *MatK* gene in four *Shorea* species (*S. bullata*, *S. fallax*, *S. kunstleri*, and *S. smithiana*), all of which grow sympatrically at Lambir Hills. Data of DNA polymorphisms and divergences of the *Shorea* species were used for testing the "isolation with migration" model of divergence (Hey and Nielsen, 2004). This recently developed population genetic model based on Bayesian and likelihood methods offers estimates of many parameters (effective population sizes of ancestral and the descendant species, rates of gene introgression from one to the other, and time of species divergence). These parameters provide historical insights into evolution of very closely related species living sympatrically. The estimates of population size were much smaller in the ancestral species than in the descendant species. Certain extents of introgression were observed in the pairs of *S. bullata*/*S. fallax*, *S. bullata*/*S. smithiana*, *S. fallax*/*S. kunstleri*, and *S. fallax*/*S. smithiana*, whereas no evidence of introgression was found in the other comparisons. The results suggest that historical gene introgression, probably having occurred at the earlier stage of the speciation, rather than ancestral polymorphisms, caused shared genetic variation and discordant phylogenetic inferences in the *Shorea* species.

In conclusion, our phylogenetic and population genetic studies showed that the *Shorea* species are characterized by lower genetic divergence and share some genetic polymorphisms among species probably by historical gene introgression. Gene introgression among different species may create novel gene combination that may result in phenotypic differentiation and adaptation to local environment. Extents of the introgression may be different among local populations where species compositions are different. Hence, conservation of local species *in situ* is very important to preserve them, considering prospective evolutionary changes in the tropical rain forests.

REFERENCES

Hey J., and Nielsen R., 2004. Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D. persimilis*, *Genetics*, 167: 747-760.